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Mate choice errors may contribute to slow spread of an invasive Eurasian longhorn beetle in North America

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Abstract

Tetropium fuscum (Coleoptera: Cerambycidae) is a Eurasian longhorn beetle and forest pest that first became invasive to Nova Scotia, Canada around 1990. In the time since its introduction, *T. fuscum* has spread only about 150 km from its point of introduction. In its invasive range, *T. fuscum* co-exists with its congener *Tetropium cinnamopterum*. Although they are ecologically similar species, *T. fuscum* tends to infest healthier trees and has a smaller host range than *T. cinnamopterum*. If they successfully interbreed, this could lead to hybrid individuals that are more problematic than either parent species. On the other hand, if *T. fuscum* can make mating errors in the field, but is not producing hybrid offspring, then this waste of mating resources could help explain the slow spread of *T. fuscum* in North America. We conducted no-choice and choice mating experiments between *T. fuscum* and *T. cinnamopterum* males and females and determined that both *T. fuscum* and *T. cinnamopterum* males make mate-choice errors with heterospecific females in a laboratory setting. Our results suggest that mating errors may play a role in the slow spread of *T. fuscum* in North America.

Keywords

Congener, hybridisation, invasion biology, mating behaviour

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Introduction

Invasive species are a threat to global biodiversity (Rhymer and Simberloff 1996; Vitousek et al. 1997) and those that successfully establish exploit resources, such as food and shelter, thereby decreasing resources available to native species. They can also act as natural enemies (predators or parasites) for the native species they encounter. Furthermore, depletion of food sources, predation or removal of an important predator by an invasive species can have catastrophic ripple effects in an ecosystem. The rate of invasion by introduced species has been steadily rising due to climate change, habitat modification, international trade (Findley and O'Rourke 2007) and globalisation in transport of unprocessed wood products (Haack 2006), allowing for accidental introductions (Allendorf et al. 2001; Sax et al. 2007; Kelly and Sullivan 2010). Invasive species are now ubiquitous (Seebens et al. 2016) and cause significant ecological and economic impacts around the globe (Vitousek et al. 1996; Pimentel et al. 2000, 2005). Nearly half of the endangered species in the USA are threatened because of competition with and predation by invasive species (Stein and Flack 1996).

Several factors determine whether an introduced species will establish itself and become invasive in a novel habitat (Ehrlich 1986; Williamson and Griffiths 1996). Understanding factors that drive invasiveness could allow us to predict and prevent potential invaders and manage those already present (Pyšek and Richardson 2010). Traits that are predictors of invasiveness across taxa include high dispersal ability (Moyle 1986; O'Connor et al. 1986; Kolar and Lodge 2001), high reproductive rates (Gallagher et al. 2014; Mathakutha et al. 2019), high competitive ability (O'Connor et al. 1986; Newsome and Noble 1986; Moyle 1986), high propagule production (O'Connor et al. 1986; Kolar and Lodge 2001), association with humans (Kolar and Lodge 2001; García-Berthou 2007; Mathakutha et al. 2019), fast growth (Newsome and Noble 1986; Kolar and Lodge 2001), ability to tolerate and adapt to a broad range of conditions (Ehrlich 1986; Moyle 1986), large body size (Ehrlich 1986; Kolar and Lodge 2001; García-Berthou 2007) and a generalist diet (Ehrlich 1986). However, the specific combination of species traits that would allow a species to invade one habitat may not extend to the same species in another habitat or a different species in that same habitat (Lodge 1991) and we still lack a fully predictive understanding of invasions and the multiple factors that can determine invasiveness.

Many species are accidentally introduced but do not establish or experience population growth sufficient to gain pest status (Williamson and Griffiths 1996). Species that successfully establish, but then undergo limited spread, such as the phloem-feeding longhorn beetle, *Tetropium fuscum* Fabricius (Coleoptera: Cerambycidae), are poorly understood and offer an interesting window on traits and ecological factors that determine invasiveness. We examine some factors that may be negatively impacting reproductive rate in *T. fuscum* and, thus, impeding its ability to invade North America.

Tetropium fuscum experienced initial success in establishment and population growth upon its introduction to North America (in or before 1990), but by 2010, it had spread only ~ 80 km from its point of entry in Halifax, Nova Scotia (Canada)

(Rhainds et al. 2011). To date, it has only been identified in one small area in the south-eastern part of the neighbouring Province of New Brunswick (CFIA 2017), an additional 70 km from its point of introduction. *T. fuscum* is native to western Europe and northern Eurasia (Juutinen 1955), including areas with climates very similar to the invasive range in Nova Scotia. It was first discovered in mature red spruce trees in Point Pleasant Park, Halifax, NS, in 1999 (Smith and Hurley 2000), but collections in the Nova Scotia Museum of Natural History indicate that it had been present since at least 1990, having been misidentified as its native counterpart *T. cinnamopterum* Kirby (Sweeney et al. 2004). In its native range, *T. fuscum* attacks predominately stressed or moribund Norway spruce (*Picea abies* (Linnaeus) Karsten) (Juutinen 1955), but in Nova Scotia, it has been observed attacking apparently healthy red spruce (*Picea rubens* Sargent), white spruce (*Picea glauca* Moench (Voss)), black spruce (*Picea mariana* (Miller) Britton, Sterns and Poggenburg) and Norway spruce (Smith and Humble 2000).

Tetropium fuscum is unusual in that the introduced population neither died out, nor saw rapid and successful expansion in North America. *T. fuscum* has established a stable population in the Halifax area, but its expansion into other parts of North America has been extremely slow (Rhainds et al. 2011). *T. fuscum*'s co-existence with the native congener *T. cinnamopterum* in the invaded range and their ecological similarities could result in Allee effects that contribute to its slow spread in North America. The two species share many similarities including phenology and preferred host plants. *Tetropium fuscum* and *T. cinnamopterum* both emerge in the spring, beginning in May and their flight period lasts until late August (Juutinen 1955). Although *T. fuscum* emerges on average 2 weeks earlier than *T. cinnamopterum*, their flight periods overlap significantly (Rhainds et al. 2011). *Tetropium fuscum* is limited to trees in the genus *Picea* (spruces), while *T. cinnamopterum*'s somewhat broader host range includes *Picea* spp. amongst other conifers (Furniss and Carolin 1980), providing plenty of opportunity for interspecific encounters. Notably, the species share the highly conserved male-produced pheromone component *S*-fuscumol, which synergises attraction of males and females of both species when combined with host (spruce) volatiles (Silk et al. 2007; Rhainds et al. 2010; Sweeney et al. 2010). Thus, pheromone blends emitted by males of one species may attract females of both species, particularly if the male is emitting from a host tree – and this sets the stage for possible mate choice errors. Mate choice also involves more local signalling; however, *T. fuscum* and *T. cinnamopterum* males both respond to cuticular hydrocarbons on the surface of females (Silk et al. 2011).

We hypothesised that *Tetropium fuscum* males, where the two species co-occur, make mate choice errors by sometimes mating with *T. cinnamopterum* females rather than with *T. fuscum* females. Such errors might be expected to be particularly common near *T. fuscum*'s range edge. Invasive species populations are often the densest at the epicentre of invasion and become more sparsely distributed closer to the range edge (Udvardy and Papp 1969; Sagarin and Gaines 2002; Sagarin et al. 2006; Mlynarek et al. 2017). Thus, near the edge of their invasive range, *T. fuscum* males are likely to encounter primarily *T. cinnamopterum* females. If such matings produce fewer or no viable, fertile offspring, then wasted mating resources would hinder population growth of *T. fuscum*. Copulation

by *Tetropium* spp. can take several hours to complete and these beetles only live for 1–4 weeks on average (Juutinen 1955). Thus, the time it takes to locate and copulate with even one female is a non-negligible proportion of the entire lifespan of a *Tetropium* male; repeated mating errors would be even more costly. We tested whether mate choice errors occur for *T. fuscum* and *T. cinnamopterum* males in the laboratory, using: 1) choice experiments reflecting mate encounters expected at the centre of the invaded range where both species are common and 2) no-choice experiments reflecting mate encounters expected at range edges where *T. fuscum* will more frequently encounter *T. cinnamopterum*.

Methods

No-choice mating experiment

Source of beetles

We obtained *T. fuscum* from a laboratory colony at the Great Lakes Forestry Centre, in Sault Ste. Marie (Ontario, Canada). We placed them in a fridge at 5 °C, in a containment lab at the Atlantic Forestry Centre, Fredericton, New Brunswick until used in experiments.

We obtained *T. cinnamopterum* from baited red spruce bolts. In April 2015, we haphazardly chose and felled 10 red spruce trees (*Picea rubens*) with a diameter at breast height of approximately 25 cm at the Acadia Research Forest, Noonan (New Brunswick, Canada; 46°0'2.99"N, 66°20'32.72"W). We cut each bole into six 120 cm long logs and arranged them in pyramid-style decks (three largest logs on the bottom, two on the second layer and one on top) to favour infestation by *T. cinnamopterum*. We attached three lures including fuscumol, ethanol and a blend of monoterpenes, as outlined by Sweeney et al. (2010), to enhance attraction and increase the likelihood of infestation. In October 2015, we took the top three logs from each deck, cut each into four 30 cm long bolts and held them outdoors in an open, but covered storage shed at the Acadia Research Forest, exposed to ambient temperatures, until late December. We brought bolts to the Atlantic Forestry Centre, 40 at a time and reared them in sealed Plexiglas cages in a quarantine facility at 20–24 °C with constant dehumidification and a 16:8 photoperiod [L:D] to obtain live adult beetles. Once beetles began to emerge (4 weeks on average), we brushed the bolts down twice per day - once in early morning and once in early afternoon - to ensure collection of beetles as close to emergence as possible. These bolts produced only *T. cinnamopterum*. We sexed the beetles upon collection and placed them immediately in the same fridge as *T. fuscum*. All beetles were individually placed in 1.5 ml microcentrifuge tubes and labelled with sex, species and emergence date.

No-choice mating protocol

We checked beetles for vigour before using them in matings. Some beetles lived longer than others and thus we held beetles for variable amounts of time; however, most beetles were used within 7 days of collection. We presented beetles with potential mates,

without choice, in Petri dishes lined with moistened filter paper. We used four treatments: 1. *T. fuscum* male with *T. fuscum* female; 2. *T. fuscum* male × *T. cinnamopterum* female; 3. *T. cinnamopterum* male × *T. cinnamopterum* female; and 4. *T. cinnamopterum* male × *T. fuscum* female (n = 85, 154, 132 and 91, respectively). We excluded any beetles with obvious deformities and attempted to match males and females by size as much as possible. After 30 minutes, we allowed any pairs that were engaged in copulation to continue to completion.

Mating behaviour

We define a mating attempt as an instance in which a male tries to mount a female and orient their genitalia together. This behaviour includes the male positioning himself dorsally and slightly posterior to the female, extending his aedeagus and attempting to connect it to the female's ovipore. Mating attempts are distinguished from instances when a male simply climbs over a female while walking around the Petri dish. Successful mating attempts are when the male and female connect through the aedeagus and ovipore. When this connection is made, there is a visible transparent tube extending from the posterior end of one beetle to the posterior end of the other. Typically, during successful copulation, female *Tetropium* run around and drag the males behind them by their genitalia.

Statistical analysis

We compared five response variables across treatments: proportion of beetle pairs attempting to mate, proportion mating successfully, time until first mating attempt, time until successful mating and time spent in copula.

As our no-choice mating experiment is essentially two independent no-choice mating experiments, one using *T. cinnamopterum* males and another using *T. fuscum* males, we ran some of the analyses for these two experiments separately. We chose to do this for the proportion of males that attempted and the proportion of males that succeeded because the comparisons we were interested in were treatment 1 (*T. cinnamopterum* male × *T. cinnamopterum* female) compared to treatment 2 (*T. cinnamopterum* male × *T. fuscum* female), as well as treatment 3 (*T. fuscum* male × *T. cinnamopterum* female) compared to treatment 4 (*T. fuscum* male × *T. fuscum* female). For each comparison, we tested the prediction that the proportion of mating attempts would be greater with conspecifics than heterospecifics, using a two-sided Fisher's Exact Test. We similarly tested a second prediction, that the proportion of pairs with successful matings would be greater with conspecifics than heterospecifics.

As both *T. fuscum* and *T. cinnamopterum* males respond behaviourally to contact pheromones present in female cuticular hydrocarbons, time until first mating attempt and time until successful mating reflect events, respectively, before and after males contact females and gain information about their identity (Silk et al. 2011). We asked whether there were differences amongst treatments in time until first mating attempt, which would reflect behaviour of *Tetropium* males before they obtain information

about cuticular hydrocarbons. We performed Box-Cox transformation of data for time until first mating attempt, using the R package bestNormalize (v. 3.3.5 2021) (Peterson and Cavanaugh 2019) to determine the most effective transformation within the Box-Cox family. The best lambda values were 0.15 for time until first mating attempt and 0.22 for time until successful mating attempt. We performed a two-way ANOVA on each response variable, using male species and female species as factors, to compare times amongst treatments. We used Tukey's HSD for pairwise comparisons where main effects were significant.

A longer time until a successful mating attempt indicates that the male is reluctant to mate with the female they are interacting with. This longer time to success, coupled with behaviour of *Tetropium* males after touching the females with their antennae prior to copulation, suggests that this reluctance is based on the female's cuticular hydrocarbon composition. Once a male had committed to mating with a particular female, we expected the time spent in copula to be the same whether with a heterospecific or conspecific female. We transformed our time-in-copula data using a hyperbolic arcsine, based on the recommendation of bestNormalize. We then tested the hypothesis with a two-way ANOVA with male species and female species as factors. We performed all statistics in R, using base R version 4.0.4 (R Core Team 2021).

Choice mating experiment

Source of beetles

In April 2016, we felled six red spruce trees (*Picea rubens*) with a mean diameter at breast height of about 25 cm from each of four sites: Acadia (NB) (46°0'2.99"N, 66°20'32.72"W), Sandy Lake (NS) (44°44'42.67"N, 63°40'40.76"W), Antrim (NS) (44°57'59.80"N, 63°22'18.58"W) and Westchester (NS) (45°36'52.86"N, 63°42'25.59"W). We also felled two additional trees of the same criteria from Acadia and transported them to a fifth site in Memramcook (NB) (46°3'8.06"N, 64°34'46.45"W). We arranged the trees into decks and baited them with pheromone as described for the no-choice mating experiment. In November 2016, we cut the top three logs from each deck into four 30 cm bolts and brought the bolts back to the Atlantic Forestry Center in Fredericton, New Brunswick. We cut up all six logs from the two Memramcook decks to increase the number of beetles we got from this site. We placed the bolts into a containment freezer at -2 °C in order to simulate winter conditions. We left the bolts in the freezer until January 2017, when we brought batches of bolts out of the freezer and warmed them up in sealed Plexiglas cages in containment facilities at 20–24 °C with constant dehumidification and a 16:8 photoperiod [L:D] to allow the beetles to develop into adults. We collected and stored the beetles as for the no-choice mating experiment.

Choice mating protocol

We checked beetles for vigour prior to their use in matings, as in the no-choice experiment. Most beetles were used within 10 days of collection. We had two treatments for

this experiment: 1. *T. fuscum* male presented with *T. fuscum* female and *T. cinnamopterum* female; and 2. *T. cinnamopterum* male presented with the same choice (n = 42 and 30, respectively). We placed the females together and placed the male directly across a Petri dish lined with moistened filter paper. We gave the males 30 minutes to begin copulating with one of the females. If, at the end of the 30-minute time period, the male was in copula with one female, we removed the other female and left the mating pair in the dish until completion of copulation. If, at the end of the 30-minute time period, the male was not in copula with a female, we removed all three beetles from the Petri dish.

Statistical analysis

We compared four response variables between treatments: time until first mating attempt, species of female first touched by male, species of female that males first attempted to mate with and species of female for successful matings.

As our choice mating experiment is essentially two independent choice mating experiments, one using *T. cinnamopterum* males and another using *T. fuscum* males, we ran some of the analyses for these two experiments separately. We chose to do this for species of first touch female and species of first female attempted because the comparisons that were meaningful to us were *T. cinnamopterum* males with conspecific females compared to heterospecific females and, separately, *T. fuscum* males with conspecific females compared to heterospecific females. For each experiment, we tested for preference of species of first-touch female using an Exact Binomial Test with p set at 0.5. In each case, we used a second Exact Binomial Test with p set at 0.5 to look at preference of species of female first attempted with. We did not do formal statistics on our time until successful mating in this experiment because of the clear-cut pattern for preference of conspecific females and the low sample size of heterospecific matings in both treatments. We calculated 95% confidence intervals for rates of heterospecific matings using a binomial CI calculator (Pezzullo 2009).

We used the R package bestNormalize (v. 3.3.5 2021) (Peterson and Cavanaugh 2019) in order to determine the most effective transformation for the data, leading us to do a logarithmic transformation. We performed a two-way ANOVA, using male species and heterospecific vs. conspecific females as factors, to compare times amongst treatments, followed by a Tukey's HSD for pairwise comparisons of significant main effects. We conducted all statistical analysis in R using base R version 4.0.4 (R Core Team 2021).

Results

No-choice mating experiment

Tetropium cinnamopterum males both attempted ($p < 2 \times 10^{-16}$) and succeeded ($p < 2 \times 10^{-16}$) significantly less with heterospecific females than with conspecific females. We

saw the same pattern with *T. fuscum* male attempts ($p = 5.81 \times 10^{-6}$) and successes ($p = 0.02$) (Fig. 1).

Neither male ($F_{1.203} = 0.83$; $p = 0.36$) nor female ($F_{1.203} = 0.58$; $p = 0.45$) species had a significant effect on time until first mating attempt (Fig. 2), but the interaction of the two was significant ($F_{1.203} = 29.77$; $p = 1.41 \times 10^{-7}$). Tukey's HSD analysis suggests that both *T. cinnamopterum* and *T. fuscum* males take significantly longer to attempt to mate with heterospecific females than conspecific females ($p = 3.03 \times 10^{-5}$, $p = 0.02$, respectively).

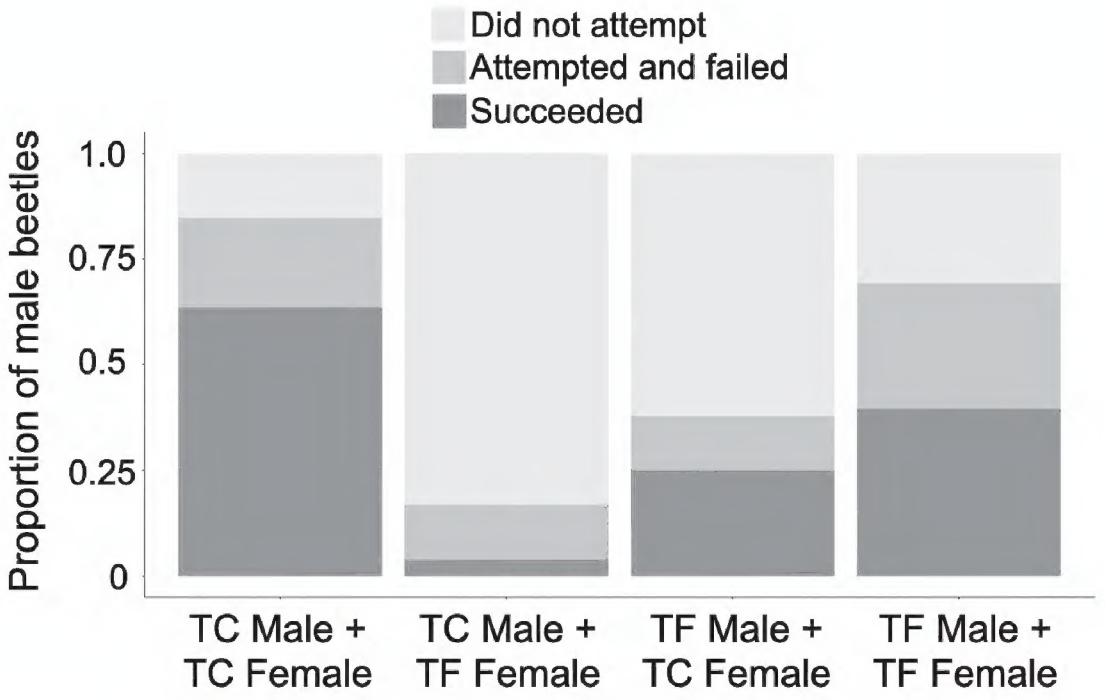

Figure 1. Proportion of *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment that did not attempt to mate, attempted to mate but failed and succeeded to mate (n = 85, 154, 132, 91).

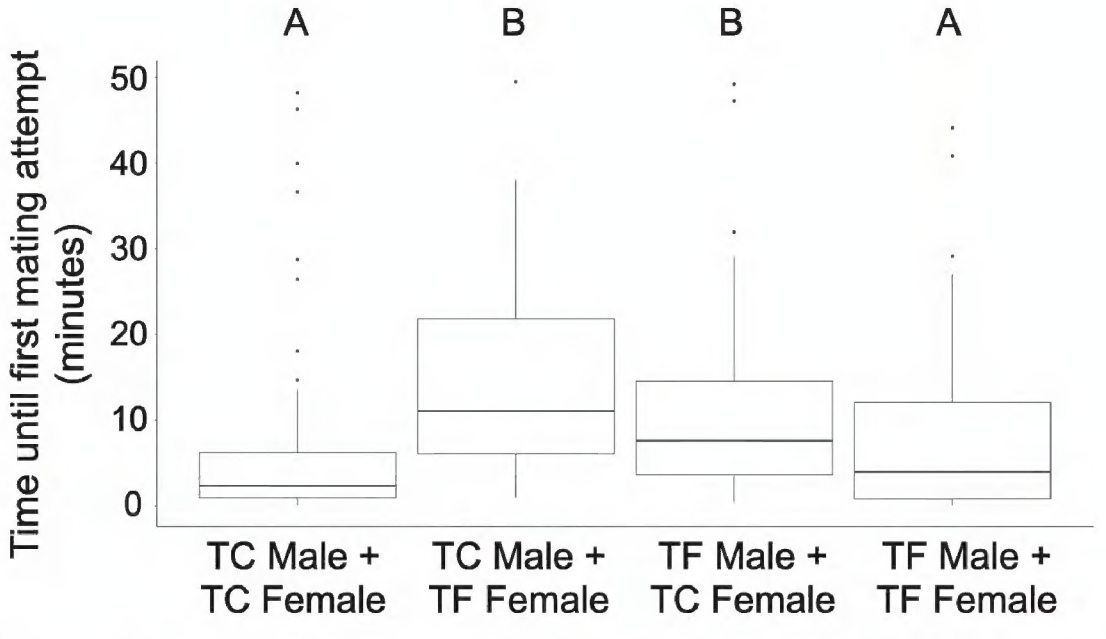

Figure 2. Time until first mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 72, 26, 50, 63, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. Boxes with different letters are significantly different (Tukey's HSD, $p < 0.05$).

Male species had no effect on time until successful mating attempt (Fig. 3; $F_{1.122}$ = 0.70; p = 0.40), nor did female species ($F_{1.122}$ = 0.17; p = 0.68), but the interaction of the two was significant ($F_{1.122}$ = 9.73; p = 2.27 × 10^{-3}). *Tetropium cinnamopterum* males took significantly longer to successfully mate with heterospecific females than conspecific (Tukey's HSD; p = 0.02), but *T. fuscum* males did not (Tukey's HSD; p = 0.66).

There was no effect of male species ($F_{1.122}$ = 0.29; p = 0.86), female species ($F_{1.122}$ = 0.61; p = 0.44) or the interaction of the two ($F_{1.122}$ = 3.49; p = 0.06) on time spent in copula (Fig. 4).

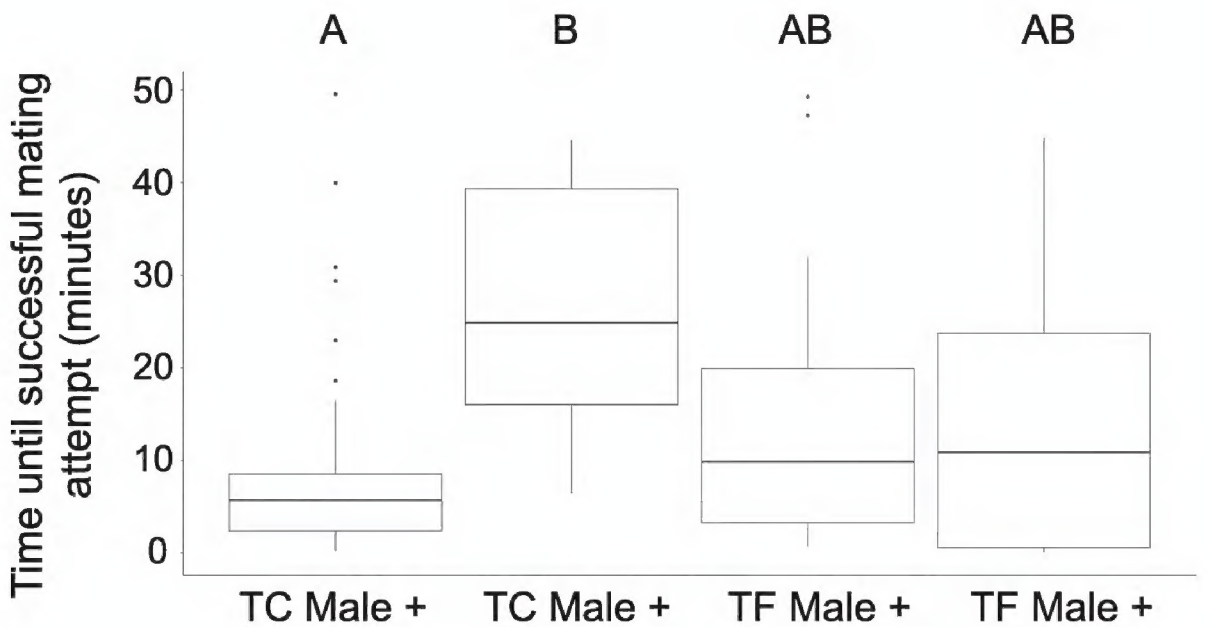

Figure 3. Time until successful mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 54, 6, 33, 37, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. Boxes with different letters are significantly different (Tukey's HSD, p < 0.05).

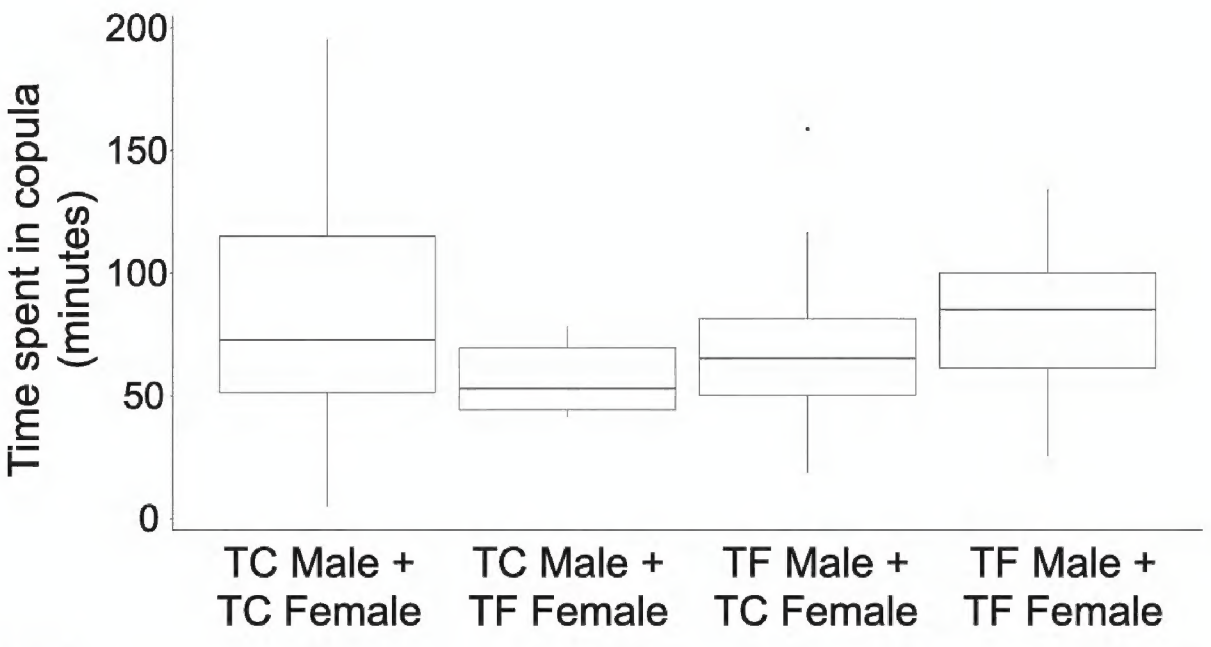

Figure 4. Time spent in copula by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a no-choice mating experiment (n = 54, 6, 33, 37, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. There were no significant differences amongst treatments.

Choice mating experiment

Species of male had no significant effect on time until first mating attempt ($F_{1.58}$ = 1.41; p = 0.24) (Fig. 5). Species of female also had no effect on time until first mating attempt for either *T. fuscum* or *T. cinnamopterum* males ($F_{1.58}$ = 0.66; p = 0.42) (Fig. 5).

Species of first touch female for *T. fuscum* males was 25 conspecific and 17 heterospecific. For *T. cinnamopterum*, it was 13 conspecific and 17 heterospecific. Neither *T. cinnamopterum* nor *T. fuscum* males showed any significant preference for conspecific or heterospecific females at first touch (p = 0.58, 0.41, respectively).

Species of female for first mating attempt for *T. fuscum* males was 28 conspecific and five heterospecific. For *T. cinnamopterum*, it was 27 conspecific and two heterospecific. Both *T. cinnamopterum* and *T. fuscum* males showed significant preference for conspecific over heterospecific females at first mating attempt (p = 1.62×10^{-6}, 5.65×10^{-6}, respectively).

Of the 42 *T. fuscum* males used in the choice mating experiment, 12 successfully mated. 11 of those 12 matings were conspecific (95% CI 0.2 – 38% heterospecific matings). Of the 30 *T. cinnamopterum* males, 17 mated successfully and all 17 were conspecific (95% CI 0 - 19.5% heterospecific matings). Despite a clear-cut pattern of both species of male preferring conspecific over heterospecific females, we cannot reject quite high rates of heterospecific choice (up to 19% even for *T. cinnamopterum*).

Discussion

We saw evidence of interspecific mating by both *Tetropium fuscum* and *T. cinnamopterum* males in the no-choice experiment. For both species, males attempted and

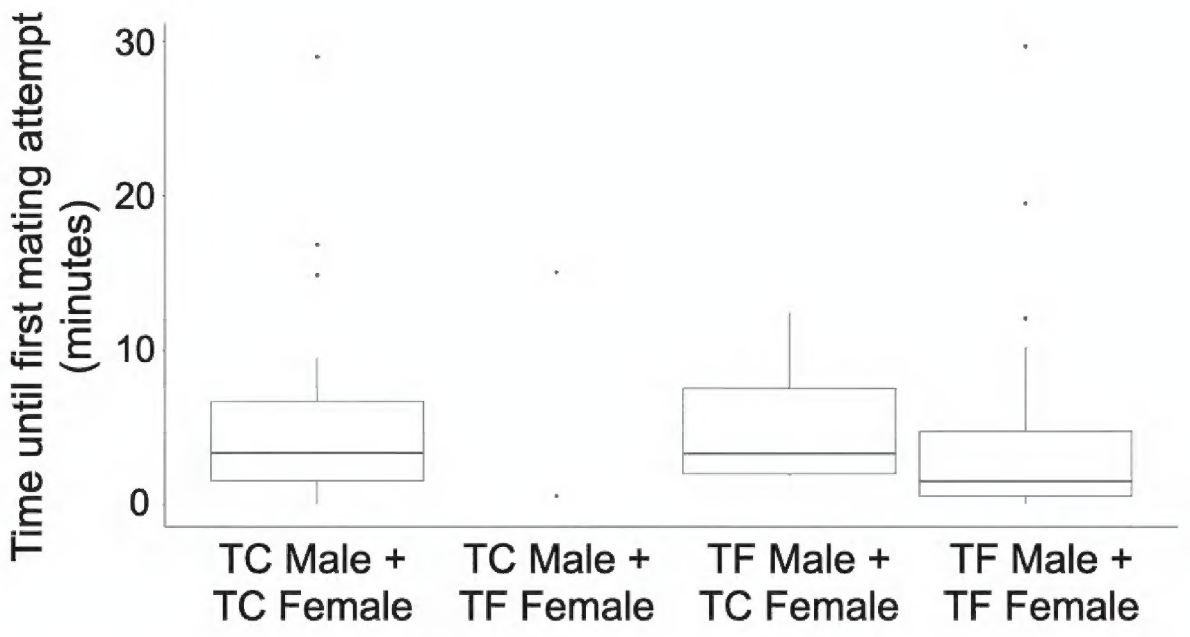

Figure 5. Time until first mating attempt by *Tetropium fuscum* (TF) and *Tetropium cinnamopterum* (TC) males in a choice mating experiment (n = 27, 2, 5, 28, respectively). Lines represent Q1-3, whiskers show +/- 1.5 × IQR and dots represent outliers. There were no significant differences amongst treatments.

succeeded significantly less with heterospecific females than with conspecific females. However, rates of heterospecific attempts and successes were both considerable. While both *T. fuscum* and *T. cinnamopterum* males took longer to attempt mating with a heterospecific female than a conspecific one, they still mated quite rapidly with heterospecific females. The same was true for time until successful mating. We often observed males touching females with their antennae prior to attempting to copulate, consistent with reports that *Tetropium* spp. males respond to female cuticular hydrocarbons (Silk et al. 2011), but inconsistent (because heterospecific matings still occurred) with a model in which a cuticular-hydrocarbon "match" is required for mating. Silk et al. (2011) also observed low percentages of heterospecific mating in both *T. fuscum* and *T. cinnamopterum* with dead females and suggested this may be due to the presence of a common cuticular hydrocarbon, 11-methylheptacosane, on the elytra of females of both species – although the overall mix of hydrocarbons differs between the species. *T. fuscum* males attempted and succeeded with heterospecific females more frequently than did *T. cinnamopterum* males, but we do not know whether this reflects lesser ability to recognise heterospecific partners or looser specificity in accepting them.

Tetropium beetles make mating errors even when they have ample opportunity to avoid them. Under choice conditions, one of twelve *T. fuscum* males mated heterospecifically. While we did not observe any heterospecific matings by *T. cinnamopterum* males in the choice experiment, our sample size was small and we cannot reject an underlying rate as high as 19%. In these choice trials, both *T. fuscum* and *T. cinnamopterum* males made first mating attempts in the same mean amount of time regardless of whether that attempt was on a heterospecific or conspecific female. We considered that perhaps males would simply mate with the first female they bumped into in the Petri dish, but in fact, first-touch female species did not adhere to any significant pattern, while both species of males preferentially made their first mating attempt on conspecific females. This indicates that males have the ability to "choose" conspecific females over heterospecific females – but they do not always do so.

Both *T. fuscum* and *T. cinnamopterum* males spent as much time in copula with heterospecific females as they did with conspecific females. This suggests that *Tetropium* males determine the suitability of a mate (imperfectly), based on the precopulatory act of touching the cuticular hydrocarbons of the female. If the barrier to copulation were something pericopulatory, like a genital lock-and-key mechanism, we would expect to see prematurely terminated copulation in heterospecific pairs. It also suggests that beetles will pay full time and resource costs of heterospecific matings, rather than breaking them off and moving on to other mating opportunities.

Our matings were all conducted in Petri dish arenas and, like any laboratory experiment, may not fully capture insect behaviour in nature. Lab experiments are commonly used to investigate arthropod mating behaviour for a wide range of arthropods including beetles (Nilsson et al 2002; Kumano et al. 2010; Rutledge and Keena 2012), moths (Jiménez-Pérez and Wang 2003; Bento et al. 2006), bed bugs (Reinhardt et al. 2009), predatory bugs (Bonte et al. 2012) and wolf spiders (Vaccaro et al. 2010). Lab experiments are particularly important for invasive species, where field manipulations

may be logistically and/or ethically problematic. Experiments under field conditions, perhaps with captive beetles released near the centre of the invasive range where such releases do not threaten to accelerate the invasion, would be worth pursuing.

While mating errors occurred under both choice and no-choice conditions, they were much more frequent in our no-choice experiments. In no-choice situations, *T. fuscum* males were more reluctant to attempt mating and less likely to successfully copulate with heterospecific females than with conspecific females; but given enough time, many of them did. This suggests that *T. fuscum* males may become less choosy the longer they go without locating a mate, a situation that may be most common at range edges. In Nova Scotia, the population density of *T. fuscum* is highest at the range centre and decreases outwards (Heustis et al. 2017; Anderson, unpublished data). At the edges of *T. fuscum*'s invasive range, then, males are more likely to encounter *T. cinnamopterum* females than *T. fuscum* females. If such hybrid matings do not produce fertile offspring, this could reinforce the edge of their range preventing the population from spreading further (Rhainds et al. 2015). Such Allee effects can limit spatial spread of a species even after establishment of a stable population (Keitt et al. 2001).

Of course, it is also possible that heterospecific matings do produce viable and fertile offspring. If so, the encounter between the two *Tetropium* species could pose a different set of challenges to forest managers. Hybrid offspring may exhibit traits intermediate to their parents (Roe et al. 2014; Patterson et al. 2017), hybrid breakdown (McQuillan et al. 2018; Pâques 2019) or hybrid vigour (Shao et al. 2019; Kumar et al. 2020). *Tetropium fuscum* attacks more vigorous trees than *T. cinnamopterum* (Smith and Humble 2000), although *T. cinnamopterum* can attack a broader range of conifers in North America than *T. fuscum* can (Furniss and Carolin 1980). Hybrid *Tetropium* might display both traits and, thus, be more threatening to North American forests than either parental species. There are similar concerns in other invasive insects. For instance, the winter moth *Operophtera brumata* Linnaeus is invasive to north-eastern North America and co-exists with its native congener *Operophtera bruceata* Hulst (Elkinton et al. 2010; Simmons et al. 2014). As in *Tetropium*, sex pheromones are highly conserved across the genus and the sex pheromone blend of *O. brumata* females attracts both *O. brumata* and *O. bruceata* males (Khrimian et al. 2010). Unsurprisingly, *O. bruceata* and *O. brumata* are known to hybridise (Elkinton et al. 2010) and, in this case, the hybrids are fertile (Havill et al. 2017). In winter moth, hybridisation between the invasive and native congeners may be aiding the spread by alleviating the Allee effects often seen in small founder populations of invasive species (Elkinton et al. 2014). Furthermore, the intermediate traits exhibited by hybrids could confer an invasive and evolutionary advantage to the hybrid offspring (Havill et al. 2017). All this suggests that it will be important to determine whether mating errors in *Tetropium* produce offspring and, if so, if those offspring are fertile and display hybrid vigour. But do they? Although very few morphologically intermediate *Tetropium* specimens have been identified in eastern Canada, morphology is not always a reliable predictor of introgression (Rhymer et al. 1994). We are currently surveying wild populations to determine whether hybrid beetles occur where the two *Tetropium* species are sympatric.

Allee effects, arising from mate-choice errors, are not the only mechanism that could be behind the slow range expansion of *T. fuscum*. Pinned edges of a species' geographical range can result from many things. Dispersal limitation can often slow an invasion, especially for species that are unlikely to be transported by humans. Restrictions on the movement of untreated lumber and firewood (Canadian Food Inspection Agency 2019) may have slowed the *Tetropium* invasion, but are unlikely to be responsible for its near cessation. More interestingly, Darwin's naturalisation hypothesis suggests that, when a species invades an area where a close relative is already established, it will be less likely to successfully establish due to higher competition for resources (Darwin 1859; Jiang et al. 2010; but see Ricciardi and Mottiar 2006; Park and Potter 2013; Sol et al. 2021) and such competition can pin range edges (Heller and Gates 1971; Bull and Possingham 1995; Case and Taper 2000). *Tetropium fuscum* may be in direct competition for resources with *T. cinnamopterum*, at least in *Picea* spp. Indeed, in Nova Scotia, *T. fuscum* has largely displaced the native *T. cinnamopterum* in the invaded zone (Dearborn et al. 2016). Furthermore, the two species are exploited by some of the same species of parasitoids, particularly in stressed spruce trees (Flaherty et al. 2011). It is perhaps most likely that a combination of factors is responsible for the apparently pinned range edge of *T. fuscum*, including competition with the native species and shared natural enemies as well as mating errors. Testing this hypothesis directly in wild populations will, unfortunately, be difficult.

Tetropium fuscum is not spreading as rapidly and destructively as other invasive forest pests, such as emerald ash borer (*Agrilus planipennis* Fairmaire). Emerald ash borer was first detected in North America in 2002, making its invasion about as old as *T. fuscum*'s, but it has already killed hundreds of millions of ash (*Fraxinus* spp.) trees in the USA alone (Herms and McCullough 2014), costs tens of billions of dollars for mitigation (Kovacs et al. 2010) and is now spreading in eastern Canada. However, our results do not mean that we should ignore the potential for future *T. fuscum* spread. Many invasive species experience a "lag phase" in which their population size and range do not increase rapidly at the beginning of the invasion (Mack 1981) while the population evolves to be better adapted to the novel environment or until environmental changes allow the species to spread (Crooks and Soulé 1999). It is important to continue the monitoring of *T. fuscum* populations in North America, so that we are not caught off guard should a sudden increase in population size or emergence of introgressed individuals become problematic.

We have demonstrated that *T. fuscum* and *T. cinnamopterum* males make mate-choice errors in the lab and we present a logical case that this may also happen in the field, especially near the edges of the invasion zone. This may well play an important role in impeding the North American spread of *T. fuscum*. If so, there are implications beyond *T. fuscum*'s invasion in particular. While some invasive species establish without any close relatives sharing their new habitat, many others, like *Tetropium*, invade alongside native congeners. Adding mate-choice errors to the list of reasons this can matter advances our understanding of why some introductions spread catastrophically, while others fade quietly away.

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